

Darwin's empirical claim and the janiform character of fitness proxies

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Abstract

Darwin's claim about natural selection is reconstructed as an empirical claim about the causal relevance of the match between the individual and its environment for the condition of the individual, and the consequence of this condition for leaving progeny. It is shown that many fitness proxies are mediating between these two steps. They are indicators of the match and predictors of reproductive success at once. Modern concepts of fitness, in contrast, are focusing exclusively on the latter. Assuming that Darwin wanted to explain selection in terms of a modern concept of fitness thus confounds his argument. Taking the janiform character of fitness proxies serious, in contrast, does not only allow for integrating Darwin's argument into current evolutionary biology, but also helps reframing and alleviating the dispute between the Modern Synthesis and the Extended Evolutionary Synthesis.

Keywords: Darwin; Extended Evolutionary Synthesis; Evolution; Fitness; Fitness Principle; Modern Synthesis; Niche Construction; Origin of Species

1. Introduction

Darwin's insight into the mechanism of evolutionary change by natural selection is often reduced to Spencer's phrase of the *survival of the fittest*. Taking fitness as the number of surviving offspring, this phrase becomes a truism. We face the situation that Darwin's insight either lacks explanatory power, or that his concept of fitness is mistaken. I reconstruct Darwin's claim about natural selection from the first edition

of the *Origin of Species* (Darwin 1859) and thus from the argument as he gave it before Spencer's phrase was included. It turns out that his claim differs drastically from the reading of Spencer's phrase as it became usual within the framework of the Modern Synthesis (MS). My reconstruction in section 2 shows that the claim has strong empirical content and that, while a notion close to fitness in the sense of population genetics can in fact be found in Darwin, this is not even closely related to what he means when using the term "the fittest". The main issue is that Darwin proposed a two-step mechanism for natural selection that involves ecological interaction, the consequences of this interaction for the condition of the individual, and the consequence of this condition for leaving progeny. It is not merely a single step from fitness to reproduction. As to be expected from a ground-breaking insight, his claim is not tautological but refutable and in need of strong empirical support. This might be one reason why the *Origin* is so rich in reported observations and discussed analogies.

Taking Darwin's empirical claim serious allows for a fresh look at the role of fitness proxies in evolutionary research, which follows in section 3. It is shown that fitness proxies of the most often used kind, like the individual growth rate, are, over and above being predictors of fitness, also measures of how well an individual matches its environment. They are janiform, looking at the same time at the physiological-ecological match and at reproductive success.

Part 4 shows how the dispute between the MS and the Extended Evolutionary Synthesis (EES) can be reconstructed as the attempt to convince the proponents of the respective other side that only one of the faces of fitness proxies is relevant. Acknowledging the janiform character of fitness proxies thus may help reframing the debate.

2. Darwin's empirical claim

2.1 Darwin's argument

Darwin's argument about the generation of biological species (Darwin 1859; 1876) is based on the idea of natural selection, which combines three ideas.¹ The first is the

¹ I am concerned only with this claim about natural selection and not with the whole argument about speciation. Though the derivation of the claim is part of the overall argumentation, to which I am alluding occasionally, it is not relevant for my present

general observation that individuals differ, and that this holds for all species. The second is the empirical finding that, in the wild, most individuals are dying at early developmental stages or at young age. The third is the theoretical result that in populations of biological individuals that produce more than one offspring during their lifetime, in the long run not all offspring can possibly survive. Let me first recapitulate this tripartite point of departure, which provides the basis of Darwin's empirical claim about evolutionary change, in reversed order.

The theoretical result at the basis of the argument is that unrestricted populations grow geometrically (i.e., exponentially), and that, if food supply grows only linearly, not all individuals can possibly survive. Darwin borrows this result from Malthus (1798, pp. 4, 6-7). In the third chapter of the *Origin of Species*, he transfers the "doctrine of Malthus" from human social systems to "the whole animal and vegetable kingdoms" and stresses that there can be neither an artificial increase of food nor "prudential restraint from marriage" in these kingdoms (Darwin 1859, p. 47). The situation therefore is that not all animals can and will survive.

This theoretical result is confirmed and specified by the empirical finding that, in the wild, most individuals die at early developmental stages or at young age. Darwin points out that many seeds and seedlings, eggs and young are "destroyed" (ibid., pp. 47, 48 *et pass.*). Not only food shortage is the reason for these deaths, though he counts it as important at least in the context of climate and seasonal changes. Relevant is also that many young individuals serve other animals as prey (ibid., p. 50).

Consequently, Darwin considers it inevitable that, in each species, many individuals die before their time, in particular before they had a chance to propagate. But this does not say anything about *which* individuals among the young ones die and *which* ones survive. Survival could be a matter of chance, of being, e.g., first or last born, or of any other account. Darwin prepares his answer to this question (which he does not ask explicitly) by referring to the general observation that individuals differ, and that this holds for all species. Variation is so important for his argument that he commences his *Origin* with two chapters on differences between individuals. In the first chapter, he describes variability as a phenomenon that allows breeders to form varieties of a species by selecting individuals for breeding that have traits deviating

purpose whether it is indeed only one or whether there are parallel arguments (Hodge 1977, 1992; Sintonen 1990; Mayr 1991; Regner 2001).

in the desired direction from other individuals. In the second chapter, he states that variation also occurs in nature and is thus not an artifact of domestication. Darwin doesn't have a satisfying explanation of variation itself, but tries to make its occurrence as plausible as he could by providing examples, both in the domesticated situation and in the wild. He discusses proposals made by other authors, namely that variation was induced by light, food excess, or other external factors. Darwin himself is cautious in ascribing these factors more than a minor influence. But he considers variation, whatever its origin might be, as a matter of fact, and most variation being heritable. (ibid., p. 10).

The theoretical result about overproduction of offspring, confirmed by the empirical result that there is indeed overproduction of offspring that is regulated by the death mainly of young individuals, leads in combination with the observation of heritable individual differences (however induced) to Darwin's central claim that exactly those individual differences will make the difference in survival: "any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relations to other organic beings and to external nature, will tend to the preservation of that individual, and will generally be inherited by its offspring. The offspring, also, will thus have a better chance of surviving" (ibid., p. 46). It follows the introduction of the term 'Natural Selection': "I have called this principle, by which each slight variation, if useful, is preserved, by the term of Natural Selection, in order to mark its relation to man's power of selection" (ibid.). Darwin conceives this process as probabilistic: "[I]f variations useful to any organic being do occur, assuredly individuals thus characterised will have *the best chance* of being preserved [...] and [...] *tend to* produce offspring similarly characterised" (Darwin 1859 p. 92, italics added). But this is merely a probabilistic weakening of the connection between "profitability" of a certain variation and survival. Which individuals survive is not a matter of pure chance.

The strength of this claim depends on how convincingly individual differences are linked to survival. Darwin conceives the link consisting in the match between the individual's traits and its environment: Survival is supported by those variations of traits that are "profitable" for the individual "in its infinitely complex relations to other organic beings and to external nature", i.e., by variations that allow the individual to cope better with its biotic and abiotic environment. In the definition, this is abridged to "being useful". Reference to the biotic and abiotic environment and to the match of the (traits of the) individual to its environment shows that *natural selection* is first of all an ecological concept. Only in combination with the

heritability of variation, which is at this point merely postulated but supported in later chapters with a plethora of empirical examples, and with the idea that the range of variation shifts so that also the limits of variability grow or shift with each new variant, that they depart further and further from the original type, as Wallace puts it in his version of a the selection theory (Wallace 1858, p. 54), it gains its evolutionary relevance.

2.3 Fit(tedness)

Darwin speaks about the profitability of certain variations for the individual's coping with its environment, which I have called above the match of the individual and its environment. This, however, is not a term Darwin uses (except in the context of breeding). He speaks sometimes of the individual or its trait as being *adapted*, in particular when stable traits of a species are at stake (Darwin 1859, pp. 2, 45, 57 *et pass.*). In more general cases and also with respect to new variations, he usually speaks of the *fit* between individual and environment. He also refers to an individual or a character as *being fitted to* or *for* the environment, or to certain ends: The flying lemur's wings are fitted for gliding through the air (*ibid.*, p. 130). Darwin admires "how infinitely complex and close-fitting [...] the mutual relations of all organic beings to each other and to their physical conditions of life" are (*ibid.*, p. 59). The fitting-relations is graded, so, e.g., seeds are better or less well fitted for dispersal (*ibid.*, p. 106). Better fit, Darwin claims, gives the individual that produces these seeds an advantage over the others (*ibid.*, p. 106).

Darwin uses the metaphor of being fitted already in his essays from 1842 and 1844, respectively, where he speaks about recent and fossil organisms as being "fitted to wholly different ends" (Darwin 1842/1844, p. 30) and, about Rhinoceroses in former times, that "some of these ancient animals were fitted to very different stations" (*ibid.*, p. 37). He writes about species being fitted to diversified means of subsistence (*ibid.*, p. 146), "best fitted to its new habits and station" (*ibid.*, p. 156) and for being "fitted to widely different ends in the economy of nature" (*ibid.*, p. 160). He uses also negations and speaks of organisms being unfit for a new climate regime (*ibid.*, p. 173) or being ill-fitted (Darwin 1859, p. 261).

In order to disambiguate Darwin's use of "being fitted", I call the degree of being fitted *to the environment* (rather than to ends or to habits, that were to be evaluated with respect to the environment anyway) the *fittedness* of an individual.

Fittedness has consequences. Darwin points out that an increase of fit increases the "chance of surviving and of leaving offspring" (*ibid.*, p. 67). So having "fitted" traits

is what makes the difference with respect to survival. The better fitting individual (or, in analogy: species) has greater chances to leave offspring than the less well fitted individual, which runs greater risk to die too early in life to leave progeny. Presupposing heritability of variation and new variation occurring in the offspring, natural selection leads to a gradual improvement of fittedness in a given environment, and to regaining fittedness after a change of the environment. So fittedness is on what natural selection acts and thus has an important explanatory role: differences in fittedness explain differences (of the chance to) leaving offspring.

The notion that fittedness is the criterion for survival and the basis for gradual changes is a strong empirical claim. Darwin presents throughout the book a lot of observational material to support this claim. From his examples we can get an idea how fittedness could be measured. Darwin obviously does not hesitate to ascribe biological functions or even purposes to traits, like flying to the bat, gliding to the flying lemur etc., and also to ascribe a lack of function, i.e., with respect to upper limb bones of whales. But this can be translated into talk about physiological capabilities. So the adequacy of the physiological capabilities to cope with the environment, e.g., to locomote and to get food, is the criterion for fittedness. An organism with wings is well fitted to an environment where the prey can best be reached via the air, one with flippers would have lower fittedness in such an environment. So we have a two-step mechanism that leads from variation to the number of progeny, and consequently a two-step explanation. Step one: Variation modifies the fittedness of an organism. Step two: the individual with higher fittedness will leave more offspring. Step one refers to physiological and ecological changes. Step two yields the evolutionary result of natural selection: individuals with a better ecological match, with higher fittedness, leave, on average, more offspring.

It is unlikely, though not impossible, that the first step of this explanation is completely and in all cases wrong, which would mean that no variation would influence how smoothly an individual can cope with its environment. The second step, however, could easily turn out to be empirically wrong, either generally or for some species, and in the latter case either in all settings or only in some particular situations. It might well be that in some species individuals that fit physiologically almost perfect into their environment have less offspring than individuals with lower fittedness. One can think of manifold reasons. They might be too lazy or too busy to build nests, unattractive for possible mates, themselves too picky in choosing mates, etc. Or they might be sterile, like mules. It is also not very likely that fittedness, which depends on many parameters of which many will be quite unstable, is a parameter that could be determined with such high precision that one could indeed order individuals unambiguously according to their fittedness. Nevertheless, Darwin

presents a highly plausible explanatory scheme and shows that it can be applied fruitfully in many cases.

2.4 Fitness: no tautology, ever

The mentioned numerical fuzziness of fittedness might have been one reason why the Modern Synthesis (cf. Huxley 1942) read Darwin's talk about fit in a completely different way than presented above and introduced the concept of fitness as the number of surviving offspring, grandoffspring, or contribution to the gene pool (which was, of course, for Darwin no accessible option) (cf. Ariew and Lewontin 2004), or, as it was proposed later on, to define fitness as the propensity (Mills and Beatty 1979; Richardson and Burian 1992; Bouchard and Rosenberg 2004). This inverts the direction of explanation: Fitness can in principle be measured and its value allows to infer how well the organism could cope with its environment, how well it is adapted. Within population genetics, fitness is indeed all one needs and fittedness would not contribute to this approach. It would not be independently accessible with its means either.

Before further contrasting the concept of fittedness with that of fitness, let me have another look at Darwin, in particular at where the point of reference for the population genetical concept of fitness can be found. This is at the same time the reference for the philosophical debate about this concept. This point of reference is related only loosely to Darwin's talk about fit, unfit and "fitted" individuals as reconstructed above. Instead, the debate is hooked to the so-called fitness principle, the phrase claiming the Survival of the Fittest, that Darwin added in the 5th edition of the *Origin* and that we find in the most popular 6th edition. He took it up from Herbert Spencer (Spencer 1864) and inserted it right behind the definition of the concept of natural selection: "But the expression often used by Mr Herbert Spencer of the Survival of the Fittest is more accurate, and is sometimes equally convenient" (Darwin 1872, p. 51).

Spencer's phrase gave rise to several severe misunderstandings and was reinterpreted again and again within varying contexts (cf. Krohs 2006). Because of its ambiguity, Thomas Henry Huxley considered it an unlucky substitution for "natural selection" (Huxley 1890). Nevertheless, it became *the* catchword of Darwin's theory, and it – rather than Darwin's extensive use of "fit" and "being fitted" – gave later on rise to the concept of fitness, which is so important in population genetics.

With a (merely stylistical) grain of salt, and detaching it from Darwin's use of "fit" and "being fitted", the phrase of the survival of the fittest can be read as the

definition of the concept of fitness: fitness is survival, to be understood from the context as long-term survival of the lineage (this being the reading of the Modern Synthesis, not of Darwin himself). And fitness is graded: if a certain individual can be said to be “the fittest”, then obviously others have lower fitness. It is also clear that the phrase is not to be read that only one, “the fittest” individual survives, so grades of fitness map on grades of survival of lineages.

Now came the philosophers, in times when only very few philosophers of biology understood biology (cf. Grene and Depew 2004), and noticed in person Karl Popper that, since fitness is the number of offspring, the fitness principle is (almost) a tautology. It merely states that the survivor survives (Popper 1974). Though often interpreted as severe criticism, Poppers position was just that evolutionary theory, being based on a tautology, is irrefutable – its core was not empirically refutable, so he took it to be a metaphysical research program (non-pejoratively used). After having been convinced that even evolutionary biology is empirical science, his way to deal with the principle was to grant it empirical content rather than to see it as a definition within the framework of the Modern Synthesis. His way out was to take fitness not as the actual number of offspring, but as the propensity, or objective probability, or stochastic disposition, to leave a certain number of offspring (Popper 1978). Popper is right, of course, that this grants empirical content to the fitness principle. There can and will be differences between objective probabilities and their actualizations – otherwise we needed no concept of probability (or propensity). But this move reduces the empirical content of evolutionary to a difference between probable and actual number of offspring. This can hardly be the correct understanding of evolutionary and I do not consider this a valid solution of the tautology problem, as do not others.

The debate about fitness being actual number of offspring (or contribution to gene pool etc.) or the corresponding propensity is still going on (e.g., Pence and Ramsey 2013; Drouet and Merlin 2015). With respect to the *Origin*, none of the two positions is correct for Darwin, but at the same time none contradicts what he says about fit. First of all: he nowhere uses the term “fitness”, in his *Origin*. Even “fittest” he uses exclusively as a part of Spencer’s phrase, never independently. It does not occur in the first edition. In the sixth edition it occurs 15 times, two times thereof in chapter headings, and, as said, in all cases as component of the ever identical phrase. This means that no passage in the *Origin* allows reading fitness, or even the abundantly used “fit”, being a label for leaving offspring (1st and 6th edition were checked). This he calls descriptively “to yield offspring”, “success in leaving progeny”, “leaving” or “producing offspring” (e.g., Darwin 1859, pp. 40/47/67; 1876 pp. 44/52/74/75) or

more specific “producing seeds” (Darwin 1859, p. 106) etc.

Let’s take stock. (1) In Darwin, we find a concept of fit or of being fitted to the environment, to habits, or to ends. It captures the match between an individual’s physiology and its environment. To disambiguate it from denoting different relations, I use “fittedness” for the match of the individual to its environment. This is an ecological, better to say, a physio-ecological concept. While Sober has called it *fitness as an ecological descriptor* (Sober 2001), I see no reason to count it as a concept of fitness at all. (2) In population genetics, we find the concept of fitness, or several related concepts of fitness, as the number of offspring or as the contribution to a gene pool, which helps explaining and predicting changes in the gene pool. Sober calls this *fitness as a mathematical predictor* (Sober 2001). Darwin, who has no need for such a numerical concept (and could not have any idea of population genetics), just describes the phenomenon as producing more or less offspring. The explanatory goals of Darwin and of population genetics are different. Darwin wanted to present an explanation how variation leads to differential reproduction, and his explanation is an ecological one. Population genetics takes it for granted that selection acts on variation, and sees no need in any independent assessment of how a phenotype matches its environment. This fittedness can, within a framework of strong adaptationsim (cf. Godfrey-Smith 2001), be directly inferred from the fitness value, without any considerations about how particular physiological traits match the environment. This is true as long as the Darwinian mechanism is not questioned. (3) Philosophy of biology has brought up the concept of fitness as propensity. The aspect of propensity occurs in Darwin as *chance* to survive and to propagate. Fitness in this reading is not identical to, but a consequence of fittedness. According to Darwin, the fit(tedness) predicts the chance to have offspring. The better the fit, the higher the chance. Fitness as propensity is a theoretical term that captures this chance. (4) The relevant empirical claim, however, is not that this propensity will on average be more or less be realized, but that fittedness gives rise to such propensity.

3. Fitness proxies

3.1 Establishing fitness proxies

Given that fitness in the sense of actual contribution to the gene pool is an important parameter in evolution research, and that fitness is often estimated by using fitness proxies, I want to show how the distinctions made above apply to present-day research, and how Darwin’s own approach helps understanding the role of fitness proxies. Proxies play quite an important role in in experimental evolution research

since determining fitness is often desired, but unfeasible. When generation time is short with respect to the observation period, fitness can in principle be measured directly or at least estimated on the basis of data directly related to reproductive success. Just to mention two examples, the contribution of an organism to the gene pool can be reconstructed by counting offspring through many filial generations, or the abundance of a genetic marker can be measured. In organisms with long generation time and long reproductive phases, things become more complicated. Measuring or estimating fitness directly is prohibited by the mismatch of the experimental and the reproductive timescale. Researchers then resort to fitness proxies – parameters that are somehow linked to fitness and allow estimating fitness even when it is not feasible to measure. Depending on the organism, candidates for fitness proxies could be, e.g., individual growth rate or annual reproductive success (Krüger et al. 2021).

The connection between annual reproductive success and fitness seems to be fairly direct, though not free of disturbance. The first might be a good estimate, but is by no means a real measure of the latter. Growth rate, however, need not be thus clearly linked to fitness. It is easy to imagine that faster growing organisms could leave even less offspring than slower growing ones, which means that the relation between the two parameters needs first to be established empirically for a species before growth rate can be taken being a proxy of fitness. In some cases it turned out to be quite good a proxy (Higginson 2020). In others, a measure of camouflage (Schielzeth, preprint) or of body condition (Milenkaya et al. 2015) were found to make up good fitness proxies.

The appropriateness of a proxy needs to be established by demonstrating that the value of the proxy co-varies with the fitness value. For understanding the roles of fitness proxies, it is helpful to look into the reasons for this. Systematic co-variation may in principle have different reasons. Fitness proxy and fitness could be causally or constitutively linked. In the case of a causal link, the proxy could be among the direct or indirect causes of fitness, it could be a direct or indirect effect of fitness, or both could be among the effects of a common cause. In the constitutive case, one could be among the constituents of the other: the proxy could be part of the basis of the emerging phenomenon called fitness, or vice versa, or both could emerge from a shared basic system.

With some of the proxies mentioned, it is quite clear that fitness depends in these cases causally on the proxy: the contribution to the future gene pool depends on the success of camouflage or on the body condition, not the other way around. With growth rate one might not want to postulate a direct causal dependence, but a

correlation brought about by a complex common cause. The number of surviving offspring depends on food intake, as does the individual growth rate. Effective foraging behavior, if it is inheritable genetically or culturally, may lead to a high individual growth rate and to survival of the offspring that also shows this behavior. At least, total offspring number at the end of life will neither cause nor constitute growth rate in early life.

These cases have in common that fitness either depends on the proxy, or on a cause of the proxy. There are other cases where an indirect measure of fitness depends on fitness itself: if the contribution to the gene pool is measured by the abundance of a unique trait, the measured parameter depends on fitness of the predecessors rather than the other way around. Usually, the measured parameter would not be called a proxy in this case, but the situation needs to be considered as one of the options nevertheless.

3.2 The two faces of fitness proxies

Many fitness proxies are physiological parameters that also depend on environmental conditions, as is obvious in the cases of individual growth rate and of camouflage. These proxies do not only face to fitness as a downstream effect, but are also indicating the physiological condition and might even be a measure of how well the individual copes with its environment – the fittedness of the organism. These janiform fitness proxies face in both directions, to fitness and to fittedness.

Concentrating on the case that the proxy is a cause of fitness or an indicator of such a cause, it is easy to see why it can be a good proxy and thus faces fitness: as long as no other causal contributions are systematically interfering, the proxy will map on fitness. Interference might easily occur, so not any causally relevant parameter is a good candidate for fitness. Breathing, for example, is a causal precondition for any offspring production in terrestrial animals. But many other factors will be more relevant for the reproduction rate and for survival of the offspring than breath rate, so that this parameter would hardly be a valid proxy of fitness. In the end, usefulness of a parameter as proxy needs to be established empirically in each case. This means that many proxies can assume their role because fitness depends on the parameter chosen as its proxy. The proxy is part of the causal mechanism that brings the contribution to the gene pool about. Due to this involvement, the proxy can be used as a predictor of fitness. This is one role of many fitness proxies.

But, as suggested above, there is a second role since many fitness proxies at the same time indicate fittedness. Growth rate, production of offspring and similar parameters obviously depend on the environment in which the organism lives. But of course

focus on the environment is too narrow a perspective. What counts as food, or as shelter, depends on the organism. How much of the food supply it can use depends on its traits and on their individual characteristic. An individual bird that has a stronger beak than its conspecifics will be able to feed on certain seeds better than the others. An eagle with weaker eyesight will gain less weight, or will gain it more slowly, than one with sharp sight. So it is not the environment, but the ease of interaction of the individual with the environment that causes quicker growth. Growth rate therefore is an indicator of how well the individual copes with the environment. In other words: it is a direct or indirect causal effect of the match of the individual with its environment. In this perspective, the fitness proxy measures the match between organism and environment, i.e., the fittedness of the organism. This is the other role of many fitness proxies.

Adaptationists may interpret the observation that the fitness proxy has this double role in the following way (several did so in personal discussions): Of course the fitness proxy measures match, but only because match is to be judged in terms of fitness anyway. There is, according to adaptationism, no fitness-independent measure of match since survival is the one and only currency in the game. But this argument mistakes the status of the proxy with respect to fitness.

As seen above, it is not only a predictor of fitness, but also an indicator of fittedness. Thanks to facing also to fittedness, the proxy assesses first of all how well the individual copes with its environment. When Darwin considers a strong beak matching with hard seeds, this holds even when the individual does not propagate. Match can be observed and investigated empirically. It neither needs to be, nor could possibly be derived from successful propagation. Biology is used to analyze even highly complex interactions, within the cell, within an organ, within an organism, and between organism and environment. That two macromolecules, say an enzyme and a nucleic acid, bind to each other and that one, e.g., catalyzes a reaction of the other with another molecule can be observed, though indirectly, by biochemical methods. We need not first look whether the reaction has a fitness effect, though we will often assume this. If a reaction turns out not increasing fitness, this will not corroborate the observation concerning match. The same with organism and environment: we have criteria of interaction to judge match. Sometimes integrity of the organism may indeed play a role: snails match with feeding on toadstools, mammals do not. This is a physiological criterion, a matter whether the organism keeps its functional integrity, not an evolutionary or population-genetical question. Only secondarily comes selection: the better matching organisms leave more surviving offspring – and this holds only statistically. If a systematic relation between proxy and reproductive success can be established, the proxy thus indicates

fitness as a propensity. The parameter that serves as a But Darwin' empirical claim seems to be confirmed fitness proxy thus measures some aspect of the fittedness of an organism and serves at the same time as a predictor of fitness. I take this being the reason why Sober can say that fitness as a propensity is a physiological descriptor (Sober 2001). However, not fitness itself is the descriptor, but the proxy, which serves at the same time, empirically confirmed rather than by definition, as an indicator of fitness as propensity. Not fitness, as Sober says, but fitness proxies have two faces. Granting Darwin's claim empirical content, this content is reflected exactly in their janiform character.

4. Fitness proxies and the debate about modern and extended synthesis

The insight in the two faces of fitness proxies helps better understanding the differences between the Modern Synthesis (MS) and the Extended Evolutionary Synthesis (EES), and it helps overcoming those differences. In this last section I first sketch how the differences between both approaches are presented by the respective proponents, and then discuss how acknowledging the janiform character of fitness proxies can help understanding better the difference and conciliating the positions.

4.1 Explanation in MS and in EES

Proponents of EES claim central roles of extra-genetic inheritance for evolutionary processes. They consider genetic adaptation (Waddington 1942) being important in fixing phenotypic changes genetically in the generations after they occurred by organism-environment-interactions. Not mutations, but phenotypic variation resulting from environmental conditions comes first. Therefore they regard plastic changes as important drivers of evolution. In general, they recognize "processes by which organisms grow and develop [...] as causes of evolution" (Laland et al. 2014).

Proponents of MS, in contrast, believe that their classical approach, in which phenotypic variation is largely driven by genetic variation, accounts adequately for all these points: they accept genetic adaptation but see a lack of empirical examples beyond processes generated experimentally. They stress that phenotypic plasticity, niche construction, inclusive inheritance and developmental bias, which were claimed by proponents of EES being not adequately accounted for in MS, "are already well integrated into evolutionary biology, where they have long provided useful insights." However, they see the processes as "add-ons' to the basic processes that produce evolutionary change: natural selection, drift, mutation,

recombination and gene flow. None of these additions is essential for evolution, but they can alter the process under certain circumstances” (Wray, Hoekstra et al. 2014).

From an external perspective, the differences stated so far seem to be merely about the abundance and importance of certain mechanism for evolution. There is genetic adaptation, there is phenotypic plasticity, but how important is it? There is niche construction, but is the extra-genetic inheritance it allows for strong enough to gain evolutionary relevance over and above its genetic basis? There are mutations and they are important for evolutionary processes, but aren't other processes driving evolution as well? Compared to the vigorousness of the debate, these differences appear almost marginal. At least they are in the end quantitative disagreements, which might better be solved by empirical research than by conceptual encounters.

But things are not that easy. Firstly, quantitative differences might result in qualitative ones so that theories starting from MS and EES assumptions, respectively, could still be fundamentally different. Secondly and much more important, the picture is not yet complete. What I left out so far is what both sides are considering as an evolutionary explanation.

The classical view of MS regards evolution as the change of gene frequencies. Accordingly, it is claimed that “what matters ultimately is not the extent of trait variation, nor even its precise mechanistic causes. What matters is the heritable differences in traits, especially those that bestow some selective advantage” (Wray, Hoekstra et al. 2014). So these proponents of MS explicitly abstain from any mechanistic explanation of evolutionary events. While not denying that there might be a causal story to be told about some evolutionary processes, like in genetic adaptation, this is classified as irrelevant. Important are only heritable differences in traits and not how they come about. This is not as narrow-minded as it might look. If evolution is the change of gene frequencies, this change seems to be fully explained by assigning a fitness value to each allele and calculate the outcome, or vice versa. From statistical mechanics it can be seen that such a stance is a fully: In order to describe what is going on in a volume of freely moving particles, you need to know the number, collision diameter, and mean energy of the particles, but not the details of how exactly a collision takes place in terms of causal or better to say quantum mechanical interactions.

EES, on the other hand, is interested exactly in these causal processes that are going on in the background of evolution on the population level. Here, “the processes by which organisms grow and develop are recognized as causes of evolution.” (Laland et al. 2014). Also this side stresses the difference and states that for MS, “these

phenomena [i.e., development, environmental plasticity and extra-genetic inheritance] are just outcomes of evolution. For the EES, they are also causes” (ibid.). Even if it might be too restricted a view about MS that it takes these phenomena just as outcomes, it is clear that such causal processes play no explanatory role in MS because they are considered being just a source of variation. They enable evolutionary processes, but do not influence the direction of evolution. The latter is left to the selective regime. EES, in contrast, aims at mechanistic explanations of how evolutionary events are brought about.

At stake in the dispute, however, is not in which field the approaches are interested, but what is disputed. MS does not deny that there are causal processes that bring part of the variation about, but merely that these processes are relevant for explaining evolution. EES does not deny that gene frequencies alter and that random variation may lead to evolutionary change, but only that all variation is random – which does not at all mean that it is directed, but only that it can be biased by causal processes, which therefore need to be acknowledged in explaining evolution. Part of these differences reduces to an empirical question: is there a significant number of cases where causal accounts of the generation of variants yield better explanations than explanations that rely fully on random variation. Linked to this quantitative question is the difference about what should count as an evolutionary explanation. Only on this level, the relevance of explanations on the level of causal processes affecting the phenotype, disputed by proponents of MS, and the preeminence of random genetic variation as disputed by adherents of EES, appear to be irreconcilable.

4.2 Fitness proxies as mediators between the two syntheses – a proxy of a conclusion

A look at the janiform character and double role of fitness proxies is helpful to better understand and perhaps even resolve the dispute. As we have seen, a proxy can be applied as predicting fitness, or as measuring the fitness of an organism to its environment. Analogously, each trait can just be accepted as being there, showing a certain range of variation so that each variant has its specific fitness value, or else be regarded as the outcome of causal interactions between the individual and its environment. If we follow Darwin and consider the fitness of an organism as explaining its survival and reproductive success, it seems natural counting causal processes that alter fitness as influencing evolution, over and above simply changing the selective regime – on the condition that this variation is heritable, be it (epi)genetically or simply by inheriting the environmental conditions that bring the variant about, and later genetic adaptation. The aspect EES adds to the classical picture of MS is thus considering match, but also mismatch, as resulting in part from

the interaction between environment and individual. This includes change of the environment by niche construction, but also change of the organism by environmental influences, that may include heterochronic effects as well as phenotypic plasticity. In Darwin's case of the earthworm (Darwin 1881) that exemplifies what we now call niche construction (Odling Smee et al. 2003; Sultan 2015), both perspectives are already present. MS was extremely successful in focusing on evolution understood as the alteration of gene pools, and omitted the aspect of causal individual mechanisms because of its disregard of any physiological account of fittedness. If fittedness is re-interpreted as reproductive success, as methodological adaptationism tends to do, one simply needs not look at the causal interactions that constitute fittedness, but concentrates exclusively on the causality of selection. MS shifted fittedness exclusively to ecology, while evolutionary biology could view everything through the pinhole of fitness. The Darwinian unity of ecology and evolution was divorced. The fittedness-side is now put forward as the EES alternative to MS. But the use of fitness proxies shows how both sides still belong together, inevitably. Any fitness proxy that is not merely a consequence of fitness, but a predictor, is at the same time measuring fittedness. MS looks exclusively for explanations on the one side, EES stresses the unequal importance of explanations on the other. Both work with fitness proxies. Time to acknowledge that explanations need to go from one side to the other rather than only starting at the middle line.

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